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BRYOPHYTES ON THE CALCAREOUS SOILS OF MUNGO NATIONAL PARK, AN ARID AREA OF SOUTHERN CENTRAL AUSTRALIA

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ABSTRACT.—Bryophytes were found to be abundant as components of microbiotic soil crusts on the calcareous soils of Mungo National Park, an arid area of southern central Australia. Six sites that reflected differences in soils, topography, and vascular plant vegetation were studied. At each site bryophytes were abundant, both in terms of number of species present and percent ground cover. Number of species present did not differ significantly between sites, but percent bryophyte cover was lower at a site on sand dunes in mallee woodland and a site on a silcrete ridge than at the four other sites. Environmental factors (soil texture, pH, conductivity, nutrient status, vascular plant vegetation, light level, leaf litter, and fire frequency) appear to play a significant part in determining bryophyte distribution. Mosses that occur at Mungo are also widespread on calcareous substrates throughout arid southern Australia.

Many of the bryophyte species present at Mungo also occur on limestones in high rainfall areas of eastern Australia. Environmental factors favoring bryophytic soil crusts in arid Australia are also present on limestones in high rainfall areas of eastern Australia and may account for the presence of many arid zone bryophyte species on limestones. In Australia there appears to be a relationship between rainfall and the ratios of acrocarpous to pleurocarpous mosses, and thallose to leafy liverworts. Recognition of calcareous soils, widespread in arid areas of southern Australia, may be possible by assessing a combination of characteristics of bryophyte assemblages.

Key words: arid lands, Australia, bryophytes, calcareous soils, limestones, microbiotic crusts.

This investigation of bryophyte distribution at Mungo National Park was undertaken as part of a wider study to determine whether there is a suite of bryophytes consistently associated with calcareous soils in Australia, and whether it is possible to determine the calcareous nature of a substrate by the associated bryophytes. Many bryophyte species that occur on limestones in the high rainfall areas of eastern Australia are more usually associated with arid areas of Australia (Downing 1992, Downing et al. 1991). This study considers the relationships between bryophytes of arid areas of southern Australia and bryophytes on limestones in the relatively high rainfall areas of eastern Australia.

Mungo National Park (33°45′S, 142°59′E, 91 m.a.s.l.) lies within the Australian arid zone (Fig. 1) and is well known for its significance in Aboriginal prehistory, with Aboriginal occupation dating back to 40,000 y.b.p. Prior to 1922 the present Mungo National Park was part of a property of 203,000 ha carrying approximately 50,000 sheep. The property was subsequently divided into smaller holdings; and, in 1978, the holding known as Mungo was purchased by the New South Wales National Parks and Wildlife Service. In 1979 Mungo was officially declared a national park and was extended in 1984 when Zanci, the adjoining property to the north, was added to the park. Sheep and cattle were removed from Mungo in 1978; their absence was important in our selection of a study area, as observations of bryophytes on limestones and siltstones at Attunga in eastern Australia indicate that the presence of sheep changes the nature of bryophyte assemblages (Downing 1992). Graetz and Tongway (1986) have shown that removal of microbiotic soil crusts by heavy grazing causes changes in soil structure and chemistry which are significant for plant growth. Overseas studies (Brotherson et al. 1983, Johansen and St. Clair 1986, Kleiner and Harper 1972) have shown that severe trampling by grazing animals can be the most damaging hazard of microbiotic crusts in North American deserts.

Lake Mungo lies on the flat plains of the Murray Basin, a shallow sedimentary basin created by subsidence at the beginning of the

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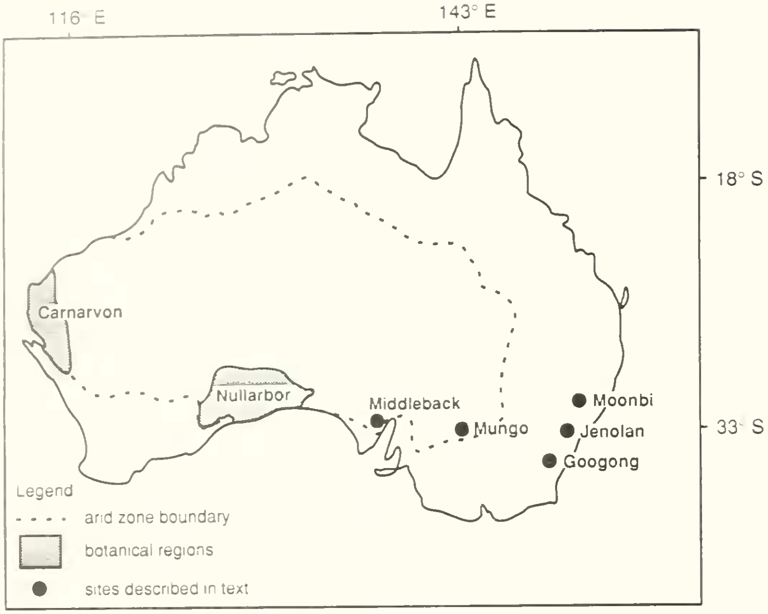

Fig. 1. Map of Australia showing location of Carnarvon and Nullarbor Botanical regions and sites described in the text in relation to the Australian Arid Zone.

Tertiary, now consisting of Quaternary aeolian sediments overlying Tertiary marine sequences (Geological Survey of NSW 1971). Fluvial and lacustrine sediments were deposited during the Pleistocene, and these are overlain by Quaternary sandy to clayey calcareous sediments, the most widespread surface geological formation of the Murray Basin (Northcote 1980).

Calcareous materials are a significant feature of the area, and calcium carbonate ($CaCO_3$) can be present (3–30%) in soils as "fine earth carbonate." Calcium carbonate can be present also as calcrete nodules, which are soft to very hard concentrations of calcium carbonate cemented soil (15–45% calcium carbonate) in a usually loose calcareous soil mix (Goudie 1983). The surface horizons of most soils in the area are alkaline, and most of the calcareous earths have pH values between 8.6 and 9.5. Deep sands are the exception and have pH values close to neutral. Sodium chloride content can be as low as 0.02% in sands, 0.05% in all other soils, with the maximum [illegible] appearing in horizons where there is the greatest [illegible] accumulation of calcium carbonate. [illegible] 0.05–0.06% in the A horizons of all [illegible] very low levels of organic matter [illegible] low [illegible] and higher in sandy loams and loams [illegible] Bradley 1982, Northcote 1980).

Phosphorus content is always low (<0.001%) and is correlated with soil texture (Northcote 1980, Stafford Smith and Morton 1990).

Lake Mungo, a vast, dry lake, is the principal landform of Mungo National Park. The lunette or crescent-shaped ridge that flanks the eastern shore of Lake Mungo and dominates the landscape is visible from the air as far as 100 km away. The base of the lunette is composed of clay, silt, and sand, topped by mobile siliceous sands.

The lake floor consists of yellow-grey cracking clays. To the west of the lake and to the southeast of the lunette are open plains of brown calcareous earths. On the northeastern side of the lunette are subparabolic dunes of siliceous sands (Eldridge 1985). A low silcrete ridge runs through the northwestern section of the lake. This is the only site within the park where rock (excluding calcrete rubble) is found, and the hard silcrete rock has been a valuable resource for stone tool manufacture by Aboriginal people.

Mungo lies within the arid zone of Australia as defined by Meigs (1953), with the southern boundary of the Australian Arid Zone following the 250-mm rainfall isohyet, the eastern and northern boundary following the 375-mm isohyet, and the Indian Ocean forming the boundary in the west (Fig. 1).

TABLE 1. Climatic data. Mean monthly maximum and minimum temperatures (°C) for Mildura, 34°14'S, 142°05'E, 95 km SW of Mungo National Park: m.max = mean maximum temperature, m.min. = mean minimum temperature (Bureau of Meteorology 1975). Average monthly rainfall in mm for Pooncarie, 33°22'S, 142°35', 56 km NW of Mungo (Bureau of Meteorology 1975). Rdays = number of rain days.

	J	F	M	A	M	J	J	A	S	O	N	D	Yearly
Temperature													
m.max (°C)	32	31	28	24	19	16	15	17	20	24	27	30	24
m.min. (°C)	17	16	14	11	7	5	4	5	7	10	12	15	10
Rainfall													
Mean (mm)	21	20	17	18	26	27	21	24	21	26	20	21	262
Median (mm)	9	8	9	10	18	19	18	20	15	18	10	11	246
Rdays	3	2	2	3	4	5	5	5	4	4	3	3	43

Mungo National Park has hot, dry summers and cool winters (Table 1—records for Mildura, closest temperature-recording station). Taking into account its more northerly location, mean monthly temperatures at Mungo are likely to be 1–2°C higher than those of Mildura. Frosts are common during the cooler months of the year.

Rainall averages for Pooncarie, 33°22'S, 142°35'E (closest rainfall recording station to Mungo; Table 1), recorded over 103 years indicate an evenly distributed rainfall (Bureau of Meteorology 1989a). However, in arid Australia, where there is considerable variation in rainfall from year to year, the mean is often much higher than the median, and thus the median rainfall value is a more reliable indicator of a typical year (Bureau of Meteorology 1989a). Mungo falls within an area of moderate to high rainfall variability (Bureau of Meteorology 1989b).

Mungo National Park lies within the Eastern Mulga Region of Arid Australia (Jessop 1981). The vegetation of Mungo National Park has been well documented by Rice (1986), who recognized four vegetation types: lakebed chenopod shrubland, *Heterodendrum/Casuarina* woodlands, mallee woodlands, and lunette vegetation.

METHODS

Six sites that reflected differences in topography, soils, and vascular plant vegetation were selected for study (Fig. 2). At each site a 10-m-long transect was set out. Along this transect, two adjacent rows of 1-m^2 quadrats were studied, giving a total of twenty 1-m^2 quadrats for each site. Direction and slope of each transect were recorded. Fieldwork was carried out in May and October 1991.

Site A: 33°43'45"S, 143°01'15"E, 98 m.a.s.l. western shore of Lake Mungo. An eroded area close to Mungo homestead and shearing shed. Calcareous brown earth soils. Chenopod shrubland with *Maireana pyramidata* (Benth.) P. G. Wilson (black blue bush) and occasional *Casuarina cristata* Miq. ssp. *pauper* (F. Muell. ex Miq.) L. A. S. Johnson (belah).

Site B: 33°44'44"S, 143°07'24"E, 68 m.a.s.l. lake floor, SW of Walls of China. Yellow-grey cracking clays. Chenopod shrubland with *Maireana pyramidata* and sparse grasses.

Site C: 33°45'10"S, 143°07'30"E, 70 m.a.s.l. lunette, eastern lake shore, N of Grand Canyon track. Yellow-grey cracking clay but with more sand on the surface than at site B. Chenopod shrubland with *Maireana pyramidata* and grasses.

Site D: 33°47'14"S, 143°07'40"E, 82 m.a.s.l. belah woodland. On the plain to the east of the lunette. Uneroded calcareous brown earth. *Heterodendrum oleifolium* Desf./*Casuarina cristata* woodland with *Maireana pyramidata* and *Enchylaena tomentosa* R. Br. as undershrubs.

Site E: 33°43'55"S, 143°10'20"E, 88 m.a.s.l. mallee/dune. Dune crest in subparabolic dunes. Red siliceous sand. Mallee woodland of *Eucalyptus socialis* F. Muell. ex Miq., *E. foecunda* Schauer, *E. dumosa* A. Cunn. ex Schauer ssp. *dumosa*, and *Triodia irritans* R. Br. var. *laxispicata* N. T. Burb. (spinifex grass).

Site F: 33°43'16"S, 143°02'26"E, 73 m.a.s.l. silcrete ridge, NW lake floor. Yellow-grey cracking clays. Outcropping silcrete rock embedded in the soil and scatterings of stone chips and flakes on the surface of the soil. Chenopod shrubland, including *Maireana pyramidata*, *M. sedifolia* (F. Muell.) P. G. Wilson (pearl blue

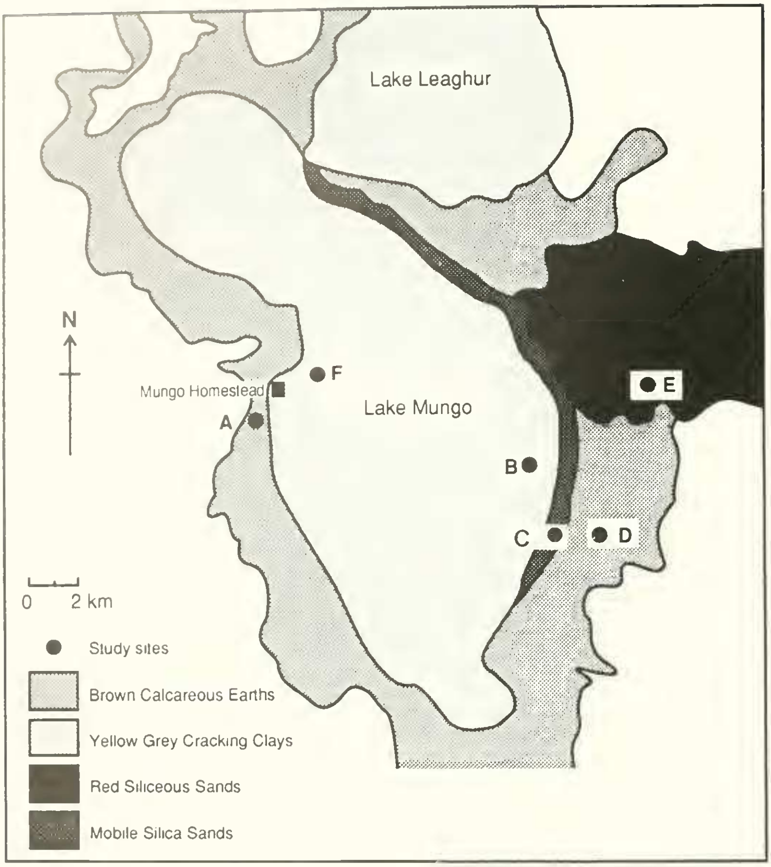

Fig. 2. Map of Lake Mungo and surroundings showing location of six study sites. A–western lake shore, B–lake floor, C–lunette, D–belah woodland, E–mallee/dune, F–silcrete ridge.

bush), and *Atriplex vesicaria* Heward ex Benth. (bladder saltbush).

Because of their small size (<5 mm), bryophytes present at Mungo could only be identified to species level after microscopic examination in the laboratory. The presence of a species within a quadrat was recorded and is referred to as an "occurrence." In addition to bryophyte species recorded from transect sites, a species list was compiled for the park. Bryophytes were collected also from a gypsum (calcium sulphate) "copi" mound, approximately 16 [illegible] of Looncarie (33°24′S, 142°41′E).

Percentage bryophyte cover was estimated for each quadrat. Estimates were also made of percent cover of bare soil, vascular plants, leaf litter, [illegible], rock (calcium carbonate nodules at some sites, silcrete rock on silcrete ridge). Soil [illegible] from the first, fifth, and tenth [illegible] samples were tested for reaction to 0.5 M HCl, for electrical conductivity, and for pH(H_2O).

Because many bryophytes of arid regions are ephemerals, additional soil was collected from each site. Pots of soil were maintained in an unshaded glasshouse at Macquarie University, watered with distilled water, and kept covered with sheets of glass to minimize invasion by glasshouse bryophyte species. Specimens growing from propagules present in the soil were recorded.

Bryophyte specimens were identified using published keys and descriptions, particularly those in Catcheside (1980), Scott (1985), Scott and Stone (1976), Beever (1988), and Sainsbury (1971). Assistance from specialists was obtained in identifying some difficult specimens. The names of bryophytes in this study for the most part follow Streimann and Curnow (1989) and Scott (1985). *Didymodon subtorquatus* (C.

TABLE 2. Number of occurrences of each species and bryophyte percent (± standard deviation) recorded from the transect at each site at Mungo National Park. A–western lake shore, B–lake floor cover, C–lunette, D–belah woodland, E–mallee/dune, F–silcrete ridge. Each transect consists of twenty 1-m² quadrats. Maximum number of occurrences possible per site = 20. ° indicates species cultivated.

Species collected	A	B	C	D	E	F	Total
1. *Didymodon torquatus*	°20	°20	°20	°20	°18	°20	118
2. *Bryum pachytheca*	°20	°19	°13	°20	°4	°17	93
3. *Desmatodon convolutus*	8	18	11	19	18	12	86
4. *Crossidium geheebii*	7	20	19	20	1	4	71
5. *Crossidium davidai*	10	12	7	17	1	11	58
6. *Aloina bifrons*	5	3	–	19	3	13	43
7. *Gigaspermum repens*	–	1		°19	12	–	32
8. *Barbula hornschuchiana*	°	4	–	°20	–	3	27
9. *Pterygoneurum ovatum*	1	4	–	8	1	–	14
10. *Bryum argenteum*	2	–	7	–	–	–	9
11. *Riccia lamellosa*	°1	°18	°	°20	°	°	39
12. *Riccia limbata*	°	°4	°	°2	°	°	6
Total number of occurrences at each site	74	123	77	184	58	80	596
Additional cultivated species							
13. *Funaria glabra*	°					°	
14. *Riccia cavernosa*		°	°	°			
15. *Riccia crystallina*		°	°	°			
Total number of species recorded for each site transect	12	13	10	13	10	10	
Bryophyte % cover ± sd	39 ± 19	28 ± 13	31 ± 12	38 ± 18	2 ± 2	9 ± 3	

Muell. & Hpe) Catches. and *Didymodon luehmannii* (Broth. & Geh.) Catches. are included in *Didymodon torquatus*. Where these species occurred together, it proved impossible to separate them into three distinct taxa. One of the most commonly occurring species of *Tortula* in Australia is usually referred to as *T. princeps* de Not., which Kramer (1988) concludes does not occur in Australia. This study follows Kramer (1988) in his use of *T. antarctica*. Distinguishing specimens of *Desmatodon convolutus* from *Crossidium davidai* proved to be extremely difficult. The number of cells of the filaments of the adaxial surface of the costa was selected as the distinguishing feature: plants with filaments consisting of one cell were assigned to *Desmatodon convolutus*, those with filaments of more than one cell to *Crossidium davidai*.

RESULTS

Bryophytes were found to be abundant components of the microbiotic soil crusts on most soils within Mungo National Park, accounting for up to 80% cover within some quadrats. The crust in most places was reddish brown and short (<2 mm high). Crustose lichens (e.g., *Psora decipiens* Hoffm.) were often a conspicuous component of the crusts. However, microbiotic crust was not present on the mobile silica dunes of the lunette nor where grasses were well established. Tongway (unpublished) has described a succession from microbiotic soil crust to grassland, which eventually leads to elimination of the microbiotic soil crust as grasses dominate the landscape.

Four sites, western lake shore (A), lake floor (B), lunette (C), and belah (D), had similar cover, with means ranging from 28% to 39% (Table 2). Two sites, mallee/dune (E, 2%) and silcrete ridge (F, 9%) had significantly less cover than the other sites and were different from each other.

A total of 15 bryophyte species were recorded from the transect sites. Ten moss species and two liverworts were collected from the transect sites. One additional moss and two additional liverworts were cultivated in the glasshouse pot trials.

There was little difference in the number of species that occurred at each site (Table 2). Two sites, the lake floor (B) and belah (D), were different from each other but had significantly more occurrences per quadrat than the western lake shore (A), lunette (C), mallee/dune (E), and silcrete (F).

The moss flora consisted exclusively of acrocarpous mosses. Pottiaceae was the dominant family, not only in number of species present, 7

TABLE 3. Bryophyte species collected at Mungo National Park and from [illegible] found at Pooncarie. ° occurred on gypsum.

Family	Taxon
POTTIACEAE	°*Aloina aloides* (Schultz) Kindb. var. *ambigua* (B.S.G.) Craig
	Aloina bifrons (De Not) Delgadillo
	Barbula crinita Schultz
	Barbula hornschuchiana Schultz
	°*Crossidium davidai* Catches.
	°*Crossidium geheebii* (Broth.) Broth.
	Desmatodon convolutus (Brid.) Grout
	Desmatodon recurvatus (Hook.) Mitt.
	°*Didymodon torquatus* (Tayl.) Catches.
	Pterygoneurum ovatum (Hedw.) Dix.
	Tortula antarctica (Hpe) Wils.
	Tortula pagorum (Milde) de Not.
	Tortula papillosa Wils.
	Trichostomopsis australasiae (Hook. & Grev.) H. Rob.
BRYACEAE	*Bryum argenteum* Hedw.
	Bryum campylothecium Tayl.
	Bryum dichotomum Hedw.
	°*Bryum pachytheca* C. Muell.
FUNARIACEAE	*Funaria glabra* Tayl.
	Funaria hygrometrica Hedw.
FISSIDENTACEAE	*Fissidens vittatus* Hook. f. & Wils.
GIGASPERMACEAE	°*Gigaspermum repens* (Hook.) Lindb.
RICCIACEAE	°*Riccia albida* Sull. ex Austin
	Riccia asprella Carring. & Pears
	°*Riccia cavernosa* Hoffm.
	Riccia crinita Taylor
	°*Riccia crystallina* L.
	Riccia lamellosa Raddi
	Riccia limbata Bisch.
	Riccia nigrella DC.
	Riccia rorida Na Thalang
	Riccia sorocarpa Bisch.

of 15 total bryophyte species, but also in number of occurrences, 419 of 596 (70%). Two species from Bryaceae accounted for 102 occurrences (17%).

The liverwort flora consisted exclusively of [illegible] from the Ricciaceae. Two species, [illegible] and *R. lamellosa*, were [illegible] from each transect site. [illegible] *tallina*, two ephemeral species, were [illegible] soil from the lake floor [illegible] and belah (D).

There [illegible] sites in terms of actual [illegible] at each transect site (Table [illegible] occurred at each transect site [illegible] species

TABLE 4. pH and EC (electrical conductivity) in 1:5 soil to water extracts (μS/cm = microsiemens/centimeter) of each transect site, and Pooncarie gypsum. + indicates soil effervesced with HCl.

Transect site	pH	EC (1:5) (μS/cm)	Reaction to 0.5 M HCl
A. Western lake shore	9.0	0.12	+
B. Lake floor	9.0	0.12	+
C. Lunette	9.0	0.05	+
D. Belah	9.0	0.06	+
E. Mallee	6.5	0.02	−
F. Silcrete	8.5	0.04	+
Pooncarie gypsum	9.0	1.51	+

accounted for 71% of total number of occurrences (426/596). *Didymodon torquatus* occurred most frequently, being present in 118 of a possible 120 quadrats. *Bryum pachytheca* occurred in 93 quadrats. *Gigaspermum repens* was recorded at three of the six sites and also on the Pooncarie gypsum.

The 32 bryophyte species collected in Mungo National Park included 22 mosses and 10 liverworts (Table 3). The moss flora consisted exclusively of acrocarpous mosses. Pottiaceae was the dominant family and was represented by 14 species. The Bryaceae consisted of 4 species, Funariaceae 2 species, and *Fissidens vittatus* and *Gigaspermum repens* were present. It is probable that other ephemeral species grow from time to time within the park. The liverwort flora consisted of 10 species of *Riccia*.

DISCUSSION

Bryophytes were abundant in most of Mungo National Park as a component of microbiotic soil crusts. Two transect sites, the lake floor and belah, had significantly greater percent cover than the other four sites. Both are situated in flat, low-lying areas with fine-textured, stable soils that retain moisture for longer periods than the more elevated, and thus more freely draining, sites on the western lake shore—lunette, mallee, and silcrete ridge. Microbiotic crusts in arid regions have consistently been shown to be more abundant (percent cover) when soil texture is finer (West 1990). Soil pH (H_2O) for all sites with the exception of the mallee/dune varied from 8.5 to 9.0, and electrical conductivity was highest for the lake floor and western lake shore, closely followed by the belah and lunette sites (Table 4). Sodium chloride is known to enhance the growth of cyanobacteria, possibly being essential for some species; thus, higher salt concentrations in the floor of the lake may in fact enhance the development of microbiotic crust (West 1990).

Two sites, the mallee/dune and silcrete ridge, had significantly less bryophyte cover than the other sites. The silcrete ridge has less soil surface area for colonization by bryophytes because of outcropping silcrete rock and scattered stone flakes. Anderson et al. (1982) found less well-developed crust on rocky and sandy sites than on sites with fine-textured soils. Despite the fact that the soils of the silcrete ridge are yellow-grey cracking clays, similar to those of the lake floor, the ridge is also 2–3 m higher than the lake floor in which it occurs, allowing free drainage and lessening the retention of water in the soil. Bryophytes were not found on, or in crevices in, the silcrete rock, but lichens were conspicuous and abundant. *Grimmia* species are often present on rock in arid or semiarid environments in South Australia and Western Australia, and the presence of this genus was anticipated in this location. The small size of the rocky outcrop and its intensive use as a stone tool quarry by Aboriginal people may have played a part in the absence of this genus from the park.

The mallee site on the dune crest had lowest bryophyte cover (2%) of all sites studied. At this site the soil consisted of coarse, sandy soil, which was highly mobile and very freely draining. Soil pH(H_2O) and electrical conductivity were significantly lower than at the other sites (Table 4). Soil pH(H_2O) of the dune sand was 6.5, significantly lower than all other sites. This parallels the work of Anderson et al. (1982), who have shown that pH and soil texture are the apparent influential variables controlling the number of lichen and moss species in microbiotic soil crusts in Utah deserts. In their studies of a semidesert region in southern Utah, they found that both species diversity and abundance increase with an increase in fine soil particles (silt and clay). On dune crests in arid Australia sand is deeper and more mobile than it is on the swales between the dunes; it also retains less moisture. The nutrient status of dune crests—calcium, nitrogen, and organic matter—is significantly lower than that of dune swales (Buckley 1981, 1982). Stafford Smith and Morton (1990) reported significantly lower levels of nitrogen and phosphorus in sand dunes than in either calcareous earths with chenopod shrublands or cracking clays. The dune soil did not effervesce with acid, indicating much lower levels of calcium carbonate in the soil than at any other site (Table 4).

The *Eucalyptus* mallee woodland of the dune crests also appears to inhibit the survival of bryophytes, with lower light levels and more leaf litter than either chenopod shrublands or *Heterodendrum oleifolium* woodlands. Mallee woodlands have a higher fire frequency than either chenopod shrublands or *Heterodendrum/Casuarina* woodlands (Gill 1989, Hodgkinson and Griffin 1982, Noble 1989). High fire frequency also reduces cryptogam cover (Greene et al. 1990). *Gigaspermum repens*, however, grows well on the loose sand of the dune crests. It may be easier for underground stems to penetrate loose, coarsely textured sand than heavier, finer-textured soils and clays. In some quadrats *G. repens* appeared to form an underground network of stems, which must play an important part in maintaining soil stability. Underground stems may also enable *G. repens* to survive fire. Two epiphytic mosses, *Tortula pagorum* and *T. papillosa*, were collected from the bark of *Heterodendrum* and *Casuarina cristata*. Both trees have thick, corrugated bark, and the accumulated dust in crevices in the bark reacted with 0.05 M HCl and had a pH of 8.5. In all cases the mosses were on either the southern side of the tree or the undersurface of a branch. In dry conditions the mosses were barely visible, but bright green leaves opened within seconds of their being doused with water. *Tortula pagorum* was also collected from rough bark on the southern side of tree trunks and the undersurface of branches of *Eucalyptus largiflorens* F. Muell. (black box) growing in box swamps on the Mungo to Pooncarie road.

Tortula antarctica, *Barbula crinita*, and *Bryum campylothecium* were present at Mungo only in protected habitats. All three occurred occasionally under the protective "skirt" on the southern side of a *Triodia irritans* var. *laxispicata* tussock and in sheltered, low-lying areas such as a terraced section of lake floor to the NW of the Mungo homestead. Two liverworts, *Riccia nigrella* and *R. sorocarpa*, were collected from this location only.

Two locations had a bryophyte assemblage that included a number of introduced and cosmopolitan species. Bryophytes collected in the vicinity of the original Mungo homestead and shearing shed included *Bryum argenteum*, *B. dichotomum* (wet area at base of a concrete tank stand), and *Trichostomopsis australasiae*. Bryophytes collected from damp sand in the vicinity of Vigars Wells, once a staging post for Cobb & Co. coaches on the NE side of the lunette, included *Bryum argenteum*, *Funaria hygrometrica*, and *Trichostomopsis australasiae*.

Six mosses and one liverwort were collected from the gypsum site at Pooncarie and two additional liverworts were cultivated (Table 3). The species list is very similar to that of Mungo National Park. Two species collected at Pooncarie, *Riccia albida* and *Aloina aloides* var. *ambigua*, were not present on the calcareous soils of Mungo National Park. Scott (1985) records the habitat for *Riccia albida* as being predominantly on gypsum-rich soils. *Aloina aloides* var. *ambigua* may be an introduced species (Catcheside 1980), and its presence may be a result of the nearby busy road and stock route.

In summary, bryophytes of Mungo National Park appear to be most abundant where soils are low lying, stable, fine textured, with high pH, high electrical conductivity, and high levels of calcium, nitrogen, phosphorus, and organic matter and where vascular plants contribute least shading (i.e., light levels are high), least leaf litter, and lowest fire frequency.

It is interesting to compare the species list of mosses collected in Mungo National Park with species lists of mosses recorded from other areas within the Australian Arid Zone. A recent study (Stoneburner et al. in press) has provided a valuable census of mosses for the Botanical Regions of Western Australia. The boundaries of two of these regions, Carnarvon and Nullarbor, approximate the boundaries of the Carnarvon and Eucla sedimentary basins respectively (Fig. 1). The calcareous soils and underlying limestone rocks that dominate these basins were deposited as marine sediments during the Tertiary. Annual rainfall is approximately 200–300 mm within the Carnarvon Botanical Region and 150–200 mm within the Nullarbor Botanical Region.

A comprehensive species list has also been assembled for Middleback Field Centre (32°57'S, 137°23'E) in southern Australia (Bell 1980, Howarth 1983). Middleback Research Station soils are aeolian sand and calcareous earth and concretions of calcium carbonate are present in many of the soils in the region. Middleback (Fig. 1) is located near the southern limit of the Australian Arid Zone, has an annual rainfall of 200 mm, and lies within the Eastern Mulga Botanical Region (Jessop 1981).

TABLE 5. Mosses of Mungo National Park and their occurrence within the Carnarvon and Nullarbor Botanical regions (Stoneburner et al. 1993) and Middleback Field Centre (Bell 1980, Howarth 1983), Australian Arid Zone. ° = present at this location.

Mungo	Carnarvon	Nullarbor	Middleback
POTTIACEAE			
Aloina aloides var. *ambigua*			
Aloina bifrons		°	°
Barbula crinita		°	°
Barbula hornschuchiana		°	°
Crossidium davidai	°	°	°
Crossidium geheebii	°	°	°
Desmatodon convolutus	°	°	°
Desmatodon recurvatus	°	°	°
Didymodon torquatus	°	°	°
Pterygoneurum ovatum	°	°	°
Tortula antarctica		°	°
Tortula pagorum		°	°
Tortula papillosa			
Trichostomopsis australasiae		°	°
BRYACEAE			
Bryum argenteum			°
Bryum campylothecium		°	°
Bryum dichotomum	°	°	°
Bryum pachytheca	°	°	°
FUNARIACEAE			
Funaria glabra			°
Funaria hygrometrica		°	°
FISSIDENTACEAE			
Fissidens vittatus	°	°	°
GIGASPERMACEAE			
Gigaspermum repens	°	°	°

There is a remarkable similarity between the assemblage of mosses at Mungo National Park and those within the Carnarvon and Nullarbor Botanical regions and at Middleback Field Centre (Table 5).

Many of the bryophytes collected from the calcareous soils of Mungo National Park are also present on limestones in high rainfall areas of eastern Australia. As at Mungo, the moss floras of three limestone sites in eastern Australia, Jenolan, Googong and Moonbi, are dominated by acrocarpous species of Pottiaceae and Bryaceae. *Didymodon torquatus*, *Gigaspermum* *repens*, and *Fissidens vittatus* are present at each limestone site. The liverwort floras of these sites consist mostly of thallose liverworts from the order Marchantiales (Downing 1992, Downing unpublished data).

A comparison of bryophytes of Mungo National Park with those of limestone sites in high rainfall areas of eastern Australia indicates many species present at Mungo are also present on eastern limestones. Jenolan (33°47′S, 150°05′E) is located 792 m.a.s.l. and has an annual rainfall of 943 mm. Googong (35°31′S, 145°16′E) is 670 m.a.s.l. with a rainfall of 640 mm per annum, and Moonbi (30°56′S, 150°56′E) is 540 m.a.s.l. with rainfall of approximately 700 mm per annum. Of the bryophyte species collected at Mungo, 52% were collected also from Googong, 63% from Moonbi and Jenolan. Comparisons for mosses alone are more striking: 62% of Mungo species were also present at Googong, 71% at Moonbi, and 76% at Jenolan Caves (Table 6). Bryophytes were also more abundant on limestone substrates, both in percent ground cover and in number of species present, than they were on nearby non-calcareous substrates (Downing 1992).

At Mungo, microbiotic crusts are best developed where the soils are fine textured and have a high pH, high electrical conductivity, high levels of calcium, phosphorus, and nitrogen, high light levels, minimal leaf litter, and low fire frequency. Limestone soils are fine textured and high in calcium; they also have a high pH and high electrical conductivity. Where caves are present in limestone, phosphorus is often deposited as bat guano (Carne and Jones 1919, Lishmund et al. 1986). Where karst is well developed, limestones provide arid microenvironments even in high rainfall areas with precipitation in excess of 2000 mm per annum (Jennings 1985). The aridity of karst geomorphology is reflected in the lack of vascular plants, particularly trees (*Eucalyptus* spp.). In their absence, light levels are high, there is minimal leaf litter (Downing 1992), and fire frequency is reduced (Holland 1993). Thus, the environmental factors that promote the abundance of bryophytes on calcareous soils in arid environments are also present on limestones in high rainfall areas of eastern Australia.

At Mungo and at each eastern limestone location, the moss flora is dominated by acrocarpous mosses, and the liverwort flora is dominated by thallose liverworts of the order Marchantiales. Pleurocarpous mosses and leafy liverworts are present on limestones only where rainfall is greater than 650 mm per annum. Two families, Pottiaceae and Bryaceae, dominate the moss flora at each site, with *Gigaspermum repens* and *Fissidens vittatus* also present (Downing et al. 1991, Downing 1992, Downing unpublished data; Table 7).

Recognition of calcareous soils in southern Australia may be possible by assessing the abundance of bryophytes. The number of species and the percent cover on calcareous soils will exceed the number of species and cover on non-calcareous soils. Acrocarpous mosses (Pottiaceae, Bryaceae) and thallose liverworts (Marchantiales) will dominate the bryoflora, and a number

TABLE 6. Mosses of Mungo National Park and their occurrence on eastern Australian limestones (Downing et al. 1991, Downing 1992, Downing unpublished data). ° = present at this location.

Mungo	Googong	Moonbi	Jenolan
POTTIACEAE			
Aloina aloides var. *ambigua*	°		
Aloina bifrons		°	°
Barbula crinita	°	°	°
Barbula hornschuchiana	°	°	
Crossidium davidai			
Crossidium geheebii	°	°	
Desmatodon convolutus			°
Desmatodon recurvatus	°		°
Didymodon torquatus	°	°	°
Pterygoneurum ovatum			
Tortula antarctica	°	°	°
Tortula pagorum	°	°	°
Tortula papillosa	°	°	°
Trichostomopsis australasiae		°	
BRYACEAE			
Bryum argenteum	°	°	°
Bryum campylothecium		°	°
Bryum dichotomum			°
Bryum pachytheca	°	°	°
FUNARIACEAE			
Funaria glabra		°	°
Funaria hygrometrica	°		°
FISSIDENTACEAE			
Fissidens vittatus	°	°	°
GIGASPERMACEAE			
Gigaspermum repens	°	°	°

TABLE 7. Summary of characteristics of bryophyte assemblages on calcareous substrates (Downing et al. 1991, Downing 1992, Downing unpublished data).

	Jenolan (943 mm per annum)	Moonbi (700 mm per annum)	Mungo (246 mm per annum)
MOSSES			
Acrocarps	78%	100%	100%
Pleurocarps	22%	0%	0%
Pottiaceae	31%	38%	44%
Bryaceae	14%	29%	13%
Gigaspermum repens	Present	Present	Present
Fissidens vittatus	Present	Present	Present
LIVERWORTS			
Leafy	Present	Absent	Absent
Thallose (Marchantiales)	Present	100%	100%

of key species will be present: *Didymodon torquatus*, *Bryum pachytheca* or *B. dichotomum*, *Gigaspermum repens*, and *Fissidens vittatus*.

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